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ORIGINAL PAPER

Omnivory and grazer functional composition moderate cascading trophic effects in experimental *Fucus vesiculosus* habitats

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Abstract We tested the relative strength of direct versus indirect effects of an aquatic omnivore depending on the functional composition of grazers by manipulating the presence of gastropod and amphipod grazers and omnivorous shrimp in outdoor mesocosms. By selectively preying upon amphipods and reducing their abundance by 70–80%, omnivorous shrimp favoured the dominance of gastropods. While gastropods were the main microalgal grazers, amphipods controlled macroalgal biomass in the experiment. However, strong predation on the amphipod by the shrimp had no significant indirect effects on macroalgal biomass, indicating that when amphipod abundances declined, complementary feeding by the omnivore on macroalgae may have suppressed a trophic cascade. Accordingly, in the absence of amphipods, the shrimp grazed significantly on green algae and thereby suppressed the diversity of the macroalgal community. Our experiment demonstrates direct consumer effects by an omnivore on both the grazer and producer trophic levels in an aquatic food web, regulated by prey availability.

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Introduction

Declines in marine top-predators and subsequent increases in mesopredators, including both medium-sized fish and crustaceans, are a global phenomenon that have shifted the trophic structure of many benthic and pelagic systems (Worm and Myers 2003; Daskalov et al. 2007; Myers et al. 2007; Casini et al. 2008; Eriksson et al. 2009). Such marine mesopredator release events may generate decreases in grazers/herbivores and cascading increases in primary producers (Scheffer et al. 2005; Vasas et al. 2007; Heithaus et al. 2008). However, this often assumes strong predator prey interactions over discrete trophic levels, while many mesopredators are omnivores that consume both secondary and primary producers and thereby can act both as mesopredators and grazers. Thus, there is an urgent need to document the different roles of omnivores in aquatic food webs to predict effects of changes in higher trophic levels.

Current interpretations of food web dynamics strongly indicate that omnivory—feeding on more than one trophic level—can stabilize complex food webs (Polis and Strong 1996; Fagan 1997; McCann et al. 1998; Neutel et al. 2002). The stabilizing effect of omnivory is supported by ecological models and mathematical analyses of real food webs, both of which show that omnivores dampen strong synchronous fluctuations in population sizes by introducing many weak trophic links (McCann et al. 1998; Neutel et al. 2002). As an increase in the number of trophic links dilute direct effects of single-species groups through the food web (Polis and Strong 1996), experimental food webs with a higher degree of omnivory are less sensitive to disturbances (Fagan 1997).

The contribution of omnivores to predator guilds, therefore, is important in determining how effects of species loss at higher trophic levels cascade down the food

web (Polis and Strong 1996; Duffy et al. 2007). Declines in apex predators can generate trophic cascades, whereby concomitant increases in mesopredator communities indirectly favour primary producers (e.g. Frank et al. 2005; Casini et al. 2008; Eriksson et al. 2009). Increased omnivory in the mesopredator trophic level may weaken trophic cascades, because omnivores may produce opposing direct and indirect impacts on lower trophic levels (Polis and Strong 1996; Pace et al. 1999; Ho and Pennings 2008). For example, omnivores that feed both on animals and plants/algae may decrease the strength of trophic cascades from predators to primary producers, by switching to grazing when herbivore abundances decline. This was demonstrated in a rocky shore mesocosm experiment, where strong trophic cascades triggered by carnivorous predators were dampened when omnivores were added to the experiments (Bruno and O'Connor 2005). Thus, omnivores may stabilize food webs exposed to loss of apex predators by preventing mesopredator-release events from cascading down the food web. However, by being less dependent on fluctuations in one single prey population, omnivores can survive on alternative foods when the preferred prey is scarce and thereby exert more persistent top–down control (Polis and Strong 1996). Omnivores also have simultaneous direct negative effects both on consumers and producers since they can act both as predators and grazers (Diehl 1993; Ho and Pennings 2008), indicating that increases in omnivore populations may have even stronger vertical effects on food webs than carnivores. Thus, because of the interplay between direct consumption and indirect positive effects, net trophic effects of omnivores are difficult to predict and probably highly dependent on prey community composition.

The aim of this study was to test the relative strength of direct versus indirect effects of an omnivorous shrimp, *Palaemon elegans*, depending on prey composition in a three-step benthic food web created in mesocosms using invertebrate grazers and algae from the Baltic Sea (Fig. 1). *Palaemon* spp. feed significantly on both crustacean mesograzers (small and mobile peracarid crustacean herbivores such as amphipods and isopods) and filamentous macroalgae (Matthiessen et al. 2007; Jephson et al. 2008; Persson et al. 2008). In the same study system, Råberg et al. (2007b) demonstrated that the functional composition of this grazer community determines algal community composition: gastropods control microalgal production and crustacean mesograzers mainly control macroalgal production. In the present experiment, we specifically test how omnivore effects interact with grazer identity, by manipulating the presence of the omnivore and the functional groups of grazers. We hypothesized that omnivore predation in our study system generates stronger direct than indirect effects on the algal community. Thus, that

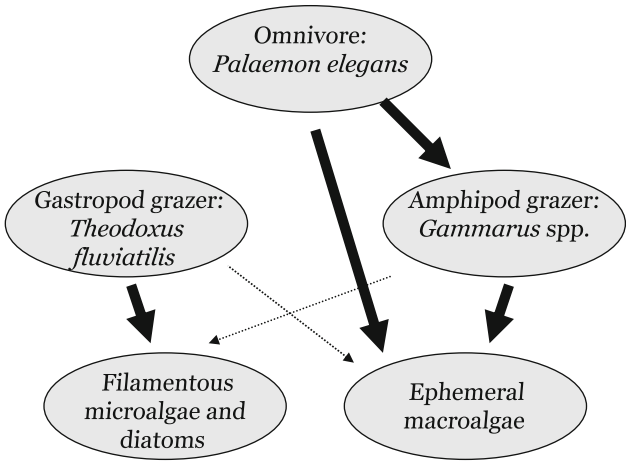

Fig. 1 Experimental food web. *Arrows* show the relative importance of feeding relations, based on (Matthiessen et al. 2007; Råberg and Kautsky 2007b; Jephson et al. 2008; Persson et al. 2008)

Palaemon does not induce a trophic cascade by reducing the grazers, but instead may compensate for declining abundances of grazer prey by significantly consuming both the grazer and algal trophic levels.

Materials and methods

We conducted the mesocosm experiment at the Askö Laboratory (58° 49′ N, 19° 39′ E) in the western Baltic Sea from 4 July to 4 August 2008. The Baltic Sea is brackish with minimal tides, and the only large, habitat-forming, perennial algae growing in the study area is *Fucus vesiculosus* (hereafter *Fucus*). In this experiment, we studied the ephemeral micro- and macroalgae and invertebrate community associated with *Fucus*, while *Fucus* itself was used as foundation habitat only. *Palaemon elegans* (hereafter *Palaemon*) was the dominant invertebrate omnivore in the area (Råberg and Kautsky 2007a). Isotope analyses suggest that it mainly consumes amphipods/isopods or ephemeral macroalgae, depending on the structure of the prey community (Jephson et al. 2008). The short-lived (~1 year) amphipod *Gammarus* spp. (hereafter *Gammarus*) was the most common crustacean grazer found in the community associated with *Fucus*. *Gammarus* reproduces continuously from spring to autumn and eggs hatch within 5–15 days (Kinne 1960). Because of its rapid reproduction, *Gammarus* should respond to changes in producer abundance (indicative of a 'dynamic' grazer) (Gruner et al. 2008). The snail *Theodoxus fluviatilis* (hereafter *Theodoxus*) was the most common gastropod in the area (Råberg and Kautsky 2007a). It is comparably longer-lived (2–3 years), and as eggs need approximately 3 months to hatch (Kirkegaard 2006), population sizes are likely to change more slowly (static) than

Gammarus. Epiphytes on *Fucus* are dominated by a mix of ephemeral cyanobacteria, microalgae (mainly diatoms and uniseriate green algae) and macroalgae (brown, green and red branched filamentous or sheet-like algae).

Specimens of *Fucus* of similar size and appearance were collected from the same area near the laboratory at a depth of 0.5 m. After removing visible fauna by hand, *Fucus* thalli were anchored to separate bricks with plastic ties and placed together for 5 days in a holding tank. By placing all *Fucus* thalli together, we allowed for exchange of invertebrate fauna between the thalli. Since all fauna cannot be removed from the *Fucus* thallus without a strong mechanical disturbance, this was important to homogenize the background start-up community in the experiment. Each thallus weighed ~300 g wet mass and had no visible epiphytes.

At the start of the experiment, one *Fucus* brick was randomly extracted from the common holding tank and placed in each of 40 circular, 30-l plastic containers (the mesocosms) standing outside and near to the shore. Although we specifically selected *Fucus* thalli that were free from visible epiphytic growth for the experiments, natural *Fucus* individuals frequently harbour a rich flora of microscopic propagules of ephemeral micro- and macroalgae. This propagule bank enhances growth of filamentous algae many times compared to sterile artificial substrates (Lotze et al. 2001; Eriksson et al. 2006). We utilized the propagule bank to get a faster response of the algal community in the mesocosms. *Fucus* is also a natural habitat for the invertebrate fauna in the area, promoting natural behaviour in the mesocosms. The cylindrical containers were supplied with a constant flow (ca. 1 l/min) of sand-filtered seawater pumped from the shore near the laboratory. Salinity and water temperature inside the containers were 6.9 (PSU) and 18° ± 2°C (observations at 14:00; maximum temperature in any container 19.8°C; air temperature of 27°C), respectively, corresponding to the natural conditions measured at the field station (unpublished data).

The experiment was designed as a factorial test of omnivore presence or absence (2 levels) and a simple diversity gradient in grazer community composition (4 levels), with 5 replicates per treatment placed in a randomized block design (40 mesocosms). For the omnivore treatment, we added three individuals of *Palaemon* (total body length = 40–50 mm) to half of the containers, which corresponded to the average number found per *Fucus* thallus in the field (unpublished data). To each omnivore treatment (no omnivore/omnivore present), four different grazer treatments were applied: (1) no grazers, (2) 500 individuals of the gastropod *Theodoxus* in a single-species assemblage, (3) 50 individuals of the amphipod *Gammarus* spp. in a single-species assemblage and (4) 250 *Theodoxus* + 25 *Gammarus* in a "both grazers present" treatment. The grazer treatments corresponded to ~1 g shell-free dry mass per mesocosm, equivalent to natural levels of shell-free biomass of grazers in the sampling area (Råberg and Kautsky 2007a). In the both grazers present treatment, the abundance ratio between *Gammarus* and *Theodoxus* (1:10) corresponded to a biomass ratio of 1:1 shell-free dry mass and was similar to the composition in the field (unpublished data). Natural populations of *Gammarus*, *Palaemon* and *Theodoxus* were collected on the same day as the experiment started and from the same area as the *Fucus* thalli. We picked experimental individuals at random, and for the grazers, we excluded individuals <5 mm. Ten per cent of the initial abundance of *Gammarus* was added twice during the experiment in order to compensate for an observed natural mortality of this species in summer (dead individuals floating at the surface).

Three weeks into the experiment (26 July), we visually estimated for each mesocosm the percentage cover of a thick growth of algae that developed on the water surface (colony forming diatoms). At the end of the experiment (after 31 days), a net bag (mesh size of 500 µm) was placed over each *Fucus* plant and attached algae (filamentous microalgae and cyanobacteria) were removed from the mesocosm sides. Water from the mesocosm was then filtered through a 300-µm sieve, retaining grazers and free-floating algae. All material was immediately frozen at −20°C. After defrosting, epiphytic algae on *Fucus* were easily removed by careful scraping, and all material was again sieved through a 300-µm sieve. We sorted the algae into three categories: (1) "attached microalgae" consisting of cyanobacteria and filamentous uniseriate microalgae that grew both epiphytically on *Fucus* and on the mesocosm sides, (2) "ephemeral macroalgae" that grew epiphytically on *Fucus* and were sorted to species level (*Ceramium tenuicorne*, *Cladophora glomerata*, *Dictyosiphon foeniculaceus*, *Pyliaella littoralis* and *Ulva* spp.) and (3) "colony forming diatoms" that grew free floating in the mesocosms (mainly of the genus *Melosira*). The diatom colonies disintegrated during freezing into smaller fragments which easily passed through the second sieving. The colony forming diatoms were therefore obtained by allowing the water that passed through the sieve to settle for 2 days; the supernatant was then aspirated and filtered through grade 595½ filters (mesh size 4–7 µm). All algae and invertebrates were dried at 80 and 60°C, respectively, for 3 days. Biomass of the ephemeral macroalgae, which only grew on the *Fucus*, was recalculated to grams of dry mass per 100 g dry mass of *Fucus*.

Experimental effects on the biomass of the canopy forming diatoms, attached microalgae and ephemeral macroalgae, and the numbers of the added grazers (*Theodoxus* and *Gammarus*) and alternative prey (other

invertebrate species: small gastropods, isopods and copepods) were analysed with factorial ANOVAs, with omnivory and grazer treatments as fixed factors and the block factor as main random effect. Predation effects on *Gammarus* and *Theodoxus* were only tested for grazer treatments where the specific grazer was added. Data were square root transformed if necessary to meet the assumptions of homogeneous variances. We analysed the diversity of ephemeral macroalgae expressed as the Shannon Wiener index using a Generalized linear model with a log-link function (Wald statistic), since the distribution did not fit the normal distribution well, even after transformations. The block factor was removed from the statistical models where block P-values > 0.50. Experimental effects on the species composition of macroalgae were analysed with a MANOVA. For algal variables with significant grazer effects (in ANOVA), we calculated effect sizes (η^2) for planned comparisons to test the relative strengths of grazer presence (grazer present or not) and grazer complementarity (*Theodoxus* vs *Gammarus*; both grazers present vs only *Theodoxus* or only *Gammarus*). For variables with significant omnivore effects, we calculated effects sizes (η^2) for planned contrasts to test the relative strength of direct and indirect effects of omnivore presence (omnivore effects in grazer treatments without and with *Gammarus* spp., respectively).

There are possible artifacts associated with using *Fucus* thalli as substrate, both regarding the behaviour of the omnivore and the grazers, and from scaling macroalgal biomass to the weight of the *Fucus* thallus. (1) Consumers strongly prefer the ephemeral micro- and macroalgae compared to the leathery *Fucus* thallus (Orav-Kotta and Kotta 2004), but when food is scarce consumers may start to feed also on *Fucus* (Hemmi et al. 2004). (2) In grazer-free conditions, strong overgrowth may hamper the growth of *Fucus* or cause degeneration of the tissue. (3) Treatments with strong grazing may promote *Fucus* growth by decreasing competition from epiphytic algae (Råberg and Kautsky 2008). We did not monitor the growth of each *Fucus* individual, but we tested for and found no systematic differences in *Fucus* biomass between treatments at the end of the experiment (no significant differences in dry weight between treatments—data not shown). Since the selection of *Fucus* thallus for the mesocosms were random, this indicates that there was no excessive growth or consumption in any treatment. We found no bite marks on *Fucus*, suggesting direct grazing was minimal (e.g. Hemmi et al. 2004). We also observed no degenerating *Fucus* thallus during the experiment. Furthermore, there was plenty of alternative algal prey during the experiment. No treatment combinations were completely devoid of micro- or macroalgae. We also tested experimental effects on ephemeral macroalgae without scaling for *Fucus* biomass, and this did not affect the results (not shown).

Results

Palaemon had strong effects on the composition of the herbivore community by preying on *Gammarus*, but not *Theodoxus* (Fig. 2). *Palaemon* suppressed *Gammarus* abundance by 72 and 79% in the both grazer present and *Gammarus* grazer treatments, respectively (Fig. 2a) (main effect of omnivore presence: $F_{1,12} = 61.87$, $P < 0.001$), but had no effect on *Theodoxus* abundance in any of the grazer treatments (Fig. 2b) (main effect of *Palaemon* presence: $F_{1,12} = 2.10$, $P = 0.17$). In the absence of *Palaemon*, *Gammarus* abundance increased from initial densities, which depended on the development of new recruits (size < 3 mm), while *Theodoxus* densities remained unchanged. Thus, *Gammarus* populations thrived with high population growth rates, whereas *Theodoxus* populations survived with low rates of recruitment (as expected from their turnover rate). Additionally, numerous alternative prey were present in the mesocosms, consisting of copepods, small gastropods (*Hydrobia* spp.) and isopods (*Idotea* spp.) that either arrived with the water supply or were associated with the *Fucus* thallus (Fig. 2c). *Palaemon* presence significantly decreased abundances of alternative prey, as the total abundance of alternative prey was 1.8 times as high in mesocosms without *Palaemon* (numbers without *Palaemon*: 128.5 ± 16.9; numbers with *Palaemon*: 71.2 ± 11.2; average per mesocosm ± SE; Table 1, Fig. 2c).

Grazer presence controlled the development of colony forming diatoms independent of the presence of *Palaemon* (Tables 1 and 2). In the treatments without grazers, diatoms (mainly of the genus *Melosira*) formed dense floating mats in the mesocosms (Supplement 1), and the biomass was 2.5 times higher compared to the average in treatments with grazers present, both with and without *Palaemon* (Fig. 3a). Grazer presence also led to a strong decrease in the biomass of attached microalgae (uniseriate green algae: *Punctaria tenuissima*, *Mougeotia* spp. and *Ulothrix* spp.; and cyanobacteria), which grew both on the sides and bottom of the mesocosm and epiphytic on the *Fucus* (Fig. 3b, Tables 1 and 2). Presence of *Theodoxus* (both in the single species and the both grazer present treatments) suppressed the biomass of attached microalgae by half compared to the *Gammarus* treatment (Fig. 3b, Table 2), indicating that *Theodoxus* was a much more effective grazer on attached microalgae than *Gammarus*. There were no significant effects of *Palaemon* on colony forming diatoms or attached microalgae (Table 1), indicating that *Palaemon* did not consume microalgae.

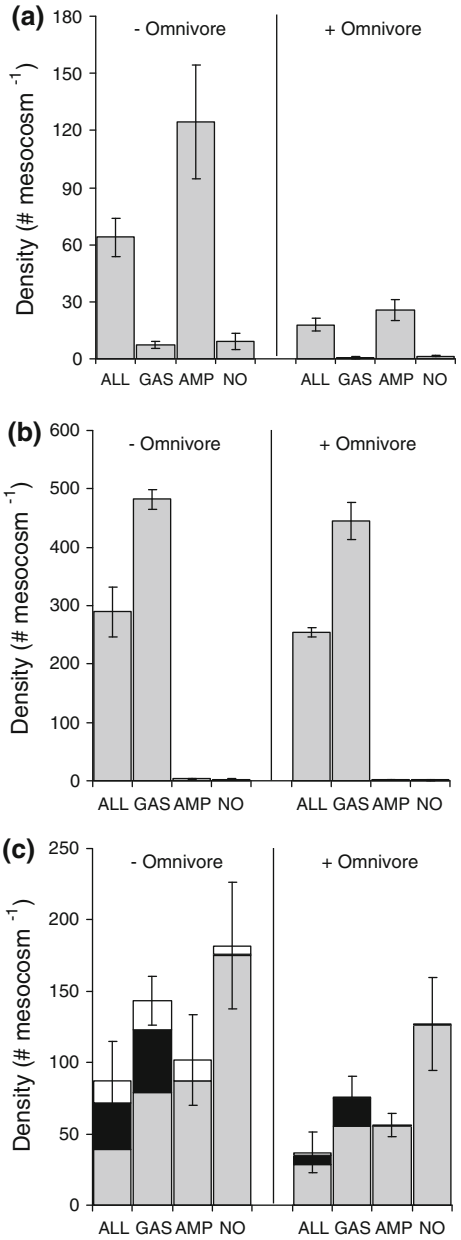

Fig. 2 Density of grazers in outdoor mesocosms after 31 days depending on the grazer identity treatment and the presence or absence of the omnivorous shrimp *Palaemon*; **a** the amphipod *Gammarus* spp., **b** the gastropod *Theodoxus* and **c** alternative prey: *grey bars* = copepods, *black bars* = small gastropods, *white bars* = isopods. Grazer treatments: ALL = adding both *Theodoxus* (250 ind.) and *Gammarus* (25 ind.), GAS = adding *Theodoxus* (500 ind.), AMP = adding *Gammarus* (50 ind.), NO = no grazers added. Means ± SE

The grazer treatments had significant effects on the total biomass of all ephemeral macroalgae (Table 1). In contrast to attached microalgae, *Gammarus* presence suppressed the macroalgal biomass by more than half compared to the *Theodoxus* treatment (Fig. 3c, Table 2), indicating strong effects of grazer identity on epiphytic micro- and macroalgae. Although Gammarus grazed significantly on macroalgae, in general grazer presence had a significantly positive effect on macroalgae compared to the no grazer treatments (Table 2), probably due to high loads both of colonial and attached filamentous microalgae outcompeting the macroalgae in the absence of grazers. Accordingly, in the treatments without grazers, there was a significant negative correlation between the cover of colonial microalgae and the biomass of the dominating ephemeral macroalgae, *Pylaiella littoralis* (Pearson product moment correlation, $r = -0.73$, $t_8 = 2.8$, $p = 0.026$).

There were no significant omnivore (*Palaemon*) effects on the total biomass of ephemeral macroalgae (Fig. 3c, Table 1). However, there was a significant interaction effect between the omnivore and grazer treatments both on the community composition of ephemeral macroalgae (significant MANOVA effect for the interaction between omnivore presence and grazer identity: $F_{10,80} = 3.45$, $P < 0.01$; Fig. 3c) and macroalgal diversity (expressed as Shannon Wiener Diversity; Fig. 3d; Table 1). *Palaemon* grazed significantly on green algae, suppressing the biomass of *Cladophora glomerata* and *Ulva* spp. in the *Theodoxus* treatment (Supplements 2 and 3, Table 3). *Palaemon* also had a positive effect on *Pylaiella littoralis* in both treatments without *Gammarus*. Presence of *Palaemon* thereby suppressed diversity of ephemeral macroalgae in the *Theodoxus* treatment by increasing the dominance of the brown alga *Pylaiella littoralis* (reducing the evenness of species diversity). Indirect effects of *Palaemon* were restricted to the red algae *Ceramium tenuicorne*, which was positively affected by *Palaemon*, but only when both *Theodoxus* and *Gammarus* were present in the treatment (Supplements 2 and 3, Table 3). Thus, we found direct negative effects of omnivore grazing on green macroalgae that affected the general diversity of the macroalgal community, and indirect positive effects restricted to one species of red macroalgae.

Discussion

In our experiment, the omnivorous shrimp *Palaemon* had significant direct effects on the composition of both the herbivore and the algal trophic levels by effectively consuming *Gammarus* and ephemeral green macroalgae. *Palaemon* decreased the density of the amphipod *Gammarus* strongly but had no effect on gastropod abundance (*Theodoxus*). In the absence of *Gammarus*, *Palaemon* also had significant effects on macroalgal community composition. By reducing green macroalgae, *Palaemon* did not suppress the total production of ephemeral macroalgae, but strongly promoted the dominance of brown algae (*Pylaiella littoralis*) and concomitantly reduced species diversity.

Table 1 General and generalized linear model results (presented by the F and Wald statistic, respectively) for the abundance of alternative prey (copepods, small gastropods and isopods) and micro- and macroalgae in response to different grazer treatments with and without omnivores

	Alternative prey (number)			Colony forming diatoms (dw)		Attached microalgae (dw)		Ephemeral macroalgae (dw)		Species diversity (H′): macroalgae	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	Wald	*P*
Omnivore presence (O)	1	9.24	0.005	1.02	0.320	0.04	0.836	2.45	0.129	4.99	0.026
Grazer identity (G)	3	5.68	0.004	16.10	0.000	28.44	0.000	8.88	0.000	0.19	0.911
O × G	3	0.20	0.895	2.60	0.070	0.60	0.621	0.80	0.504	7.72	0.021
Block	4	2.38	0.077	–	–	–	–	2.59	0.059	6.91	0.141
Error	28										

If the block factor appeared $P > 0.50$, it was removed from the statistical model

Table 2 Statistical results and effect sizes (η^2) from planned comparisons of grazer effects within the general linear models describing experimental effects on the biomass of micro- and macroalgae

	Colony forming diatoms				Attached microalgae			Ephemeral macroalgae		
Effect	*df*	*F*	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Grazer presence										
ALL and GAS and AMP vs NO	1	45.68	<0.001	−0.52	58.89	<0.001	−0.50	5.30	0.029	+0.08
Grazer complementarity										
GAS vs AMP	1	0.71	0.406	0.01	13.56	0.001	−0.11	12.91	0.001	+0.19
ALL vs GAS and AMP	1	1.92	0.176	0.02	12.87	0.001	−0.26	8.43	0.007	−0.13
ALL vs AMP	1	2.63	0.115	0.03	24.48	<0.001	−0.21	0.52	0.479	0.01
ALL vs GAS	1	0.61	0.441	0.01	1.60	0.215	0.01	18.58	<0.001	−0.28

Signs indicate direction of significant grazer effects

For general GLM results, see Table 1

Grazer treatments: *ALL* adding both *Theodoxus* and *Gammarus*, *GAS* adding *Theodoxus*, *AMP* adding *Gammarus*, *NO* no grazers added

Alternative prey was present in all treatment combinations suggesting that experimental effects were not caused by experimentally induced starving. Thus, we demonstrate that vertical food web effects of an omnivore depend on the functional composition of grazers, where the relative amount of consumption on the grazer and algal trophic levels by *Palaemon* depended on the availability of amphipod prey.

We documented no significant indirect predation effects by *Palaemon* on total primary biomass in the experiment. However, there was a significant positive effect of *Palaemon* presence on the red algae *Ceramium tenuicorne* when both grazers were present, which may have been caused by *Palaemon* predation. Thus, we demonstrated a species cascade from including the omnivorous shrimp on one macroalgal species, but no community-wide trophic cascade on the total biomass of the macroalgal community. *Palaemon* decreased the abundance of *Gammarus* by 80% and *Gammarus*, in turn, decreased the total biomass of ephemeral macroalgae to a third. This indicates potential for a strong reciprocal relationship between these three groups. This is supported by other experiments in which *Palaemon*, through strong predation on *Gammarus locusta,* induced trophic cascades that led to an increase in macroalgal biomass up to seven times, when allowed to become the dominant predator (Moksnes et al. 2008; Persson et al. 2008). However, in our experiment, direct grazing effects by *Palaemon* on green macroalgae determined the macroalgae community in the grazer treatment without *Gammarus*. This indicates that *Palaemon* may have suppressed the development of a community-wide trophic cascade by grazing on green macroalgae when the abundance of *Gammarus* decreased (no change in the total biomass of ephemeral macroalgae in the treatments with *Gammarus*). We found no direct grazing effects of *Palaemon* on *C. tenuicorne*, which may explain the significant positive indirect effects of *Palaemon* on this species (significant species cascade). Interestingly, isotope analyses show that *Palaemon* can modify their food preferences, consuming mainly grazers in some areas and mainly ephemeral macroalgae in other areas, perhaps depending on the availability of smaller sizes of mesograzer prey (Jephson et al. 2008; Persson et al. 2008). Thus, our experiment supports the role of omnivory in suppressing

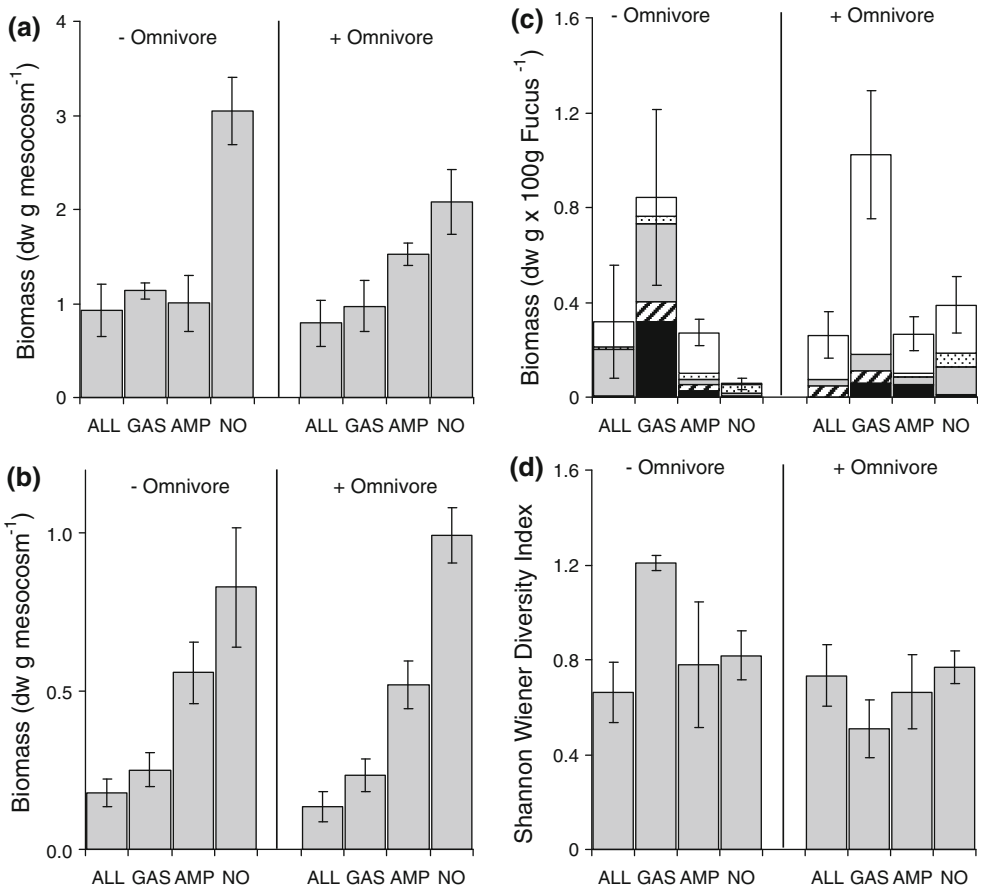

Fig. 3 Abundance of algae in outdoor mesocosms after 31 days depending on the grazer treatment and the presence or absence of the omnivorous shrimp *Palaemon*; **a** biomass of colony forming diatoms in water, **b** biomass of attached microalgae, **c** biomass of ephemeral macroalgae: *white bars* = *Pylaiella littoralis*; *dotted bars* = *Ulva* spp.; *grey bars* = *Dictyosiphon foeniculaceus*; *striped bars* = *Ceramium tenuicorne*; *black bars* = *Cladophora glomerata*, **d** species diversity of ephemeral macroalgae. Grazer treatments: ALL = adding both *Theodoxus* (250 ind.) and *Gammarus* (25 ind.), GAS = adding *Theodoxus* (500 ind.), AMP = adding *Gammarus* (50 ind.), NO = no grazers added. Means ± SE

Table 3 Statistical results and effect sizes (η^2) from planned comparisons of direct and indirect effects of *Palaemon* spp. within the general linear models describing experimental effects on the biomass of individual macroalgal species

Omnivore effects	*Ceramium tenuicorne*				*Cladophora glomerata*			*Dictyosiphon foeniculaceus*			*Pyliaella littoralis*			*Ulva* spp.		
	df	*F*	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Direct consumption																
NO (No Grazer)	1	0.21	0.653	0.00	0.12	0.728	0.00	0.37	0.546	0.01	10.86	0.003	+0.11	0.40	0.533	0.01
GAS (*Theodoxus*)	1	1.58	0.220	0.02	13.67	0.001	−0.17	1.88	0.182	0.05	25.95	<0.001	+0.25	6.69	0.015	−0.13
Indirect predation																
AMP (*Gammarus*)	1	1.55	0.223	0.02	0.19	0.670	0.00	0.24	0.630	0.01	0.57	0.458	0.01	0.38	0.545	0.01
ALL (both Grazers)	1	8.54	0.007	+0.12	0.00	0.998	0.00	0.82	0.374	0.02	1.04	0.316	0.01	0.40	0.533	0.01

Signs indicate the direction of significant omnivore effects

For general GLM results, see Supplement 2

Direct effects = effects of *Palaemon* presence in grazer identity treatments without *Gammarus* spp. (GAS and NO). Indirect effects = effects of *Palaemon* presence in grazer identity treatments with *Gammarus* spp. (AMP and ALL)

trophic cascades when omnivores compensate for their predation effects on herbivores through their ability to graze on primary producers.

In general, herbivores benefit producer evenness in marine systems (Hillebrand 2003; Hillebrand et al. 2007). However, the broad interpretation generally applies to

systems with one strong dominant species that is sensitive to grazing (e.g. Altieri et al. 2009), whereas in our study system, grazing instead promoted dominance by one macroalgal species (*Pylaiella littoralis*). Dominance determines the distribution of traits in a community, and species evenness may therefore have a stronger effect on community function than species richness (which determines the number of traits) (Hillebrand et al. 2008). In our experiment, there was no relation between species dominance and the accumulation of macroalgal community biomass. However, species evenness of natural macroalgal communities tend to increase production but not necessarily standing biomass (Altieri et al. 2009; Arenas et al. 2009), which indicate that the documented interaction between grazers and macroalgae dominance in our experiment may have significant long-term effects on the function of the community. Like many brown algae, *P. littoralis* exudes toxic substances that may deter herbivores (Råberg et al. 2005), and this may explain the dominance of *P. littoralis* in treatments with a high grazing pressure. Although the omnivore *Palaemon* demonstrated the same complementary grazing function on macroalgal structure as the mesograzer *Gammarus*, *Palaemon* promoted *P.littoralis* dominance even more. This can be seen in the uncontrolled increase in macroalgal biomass in the omnivore treatment without *Gammarus*, when *P. littoralis* escaped top–down control. Similar positive effects were demonstrated on brown algae by omnivorous benthic fish when the main mesograzer amphipod (*Ampithoe longimana*) was removed (Duffy and Hay 2000). Our results fit simple model predictions stating that a herbivore must exploit the common resource with a higher efficiency than an omnivore to enable coexistence in an omnivorous three-level food web (Polis and Holt 1992; Diehl 1993).

The degree of diet overlap by gastropod and crustacean grazers determined the structure of the algal community. Our study confirms earlier results that grazer identity determines algal community composition and production (Råberg and Kautsky 2007b): the gastropod *Theodoxus* grazed more on microalgae, and the amphipod *Gammarus* controlled macroalgae. There were no significant differences in production of microalgae between the both grazer present and the *Theodoxus* treatment, and no significant differences in production of macroalgae between the both grazer present and the *Gammarus* treatment. This demonstrates the strong species identity effects on grazing rates predicted by theoretical models (Symstad et al. 1998; Loreau and Hector 2001). However, both functional groups of mesograzers were needed to control both the macro- and microalgal production, demonstrating complementarity effects on top–down control in aquatic systems by resource partitioning between grazer groups shown by other studies (Duffy et al. 2003; Råberg and Kautsky 2007b). In absence of both functional groups of mesograzers, a thick layer of colonial microalgae developed on the surface of the mesocosms. This phenomenon is common in sheltered bays in the study area, and our results support that idea that some of the variation in natural algal blooms can be explained by different grazing rates (Eriksson et al. 2009). Moreover, our results indicated a strong trade-off between palatability and the ability to respond to resource fluctuations between the functional groups of mesograzers. For example, *Theodoxus* abundance was constant throughout the experiment, and we detected no significant predation effects by the omnivore and no new recruitment into the mesocosms. *Gammarus*, on the other hand, was heavily decimated by omnivore predation, but also showed a strong recruitment of new individuals into the mesocosms. Thus, *Theodoxus* is a 'static grazer' with little capacity to quickly change population size in response to favourable changes in the environment, but at the same time comparably resistant to predation. *Gammarus*, on the other hand, is more a 'dynamic' grazer with the capacity to quickly change population size, but was comparably sensitive to predation.

Our experiment demonstrates two properties of food webs that prevent community level trophic cascades: (1) strong direct effects by omnivores on more than one trophic levels and (2) a diversified prey community where at least one dominant grazer is tolerant to predation. The ability to feed on alternative prey makes omnivores less dependent on fluctuations in single prey populations, which promote persistence and may intensify top–down control (Polis and Strong 1996; Eubanks and Denno 1999). In some systems, strong top–down control by omnivores also translates to strong trophic cascades on plant or algal biomass, e.g. as demonstrated in salt marsh and seagrass ecosystems (Ho and Pennings 2008; Moksnes et al. 2008). In both the salt marsh and seagrass example, the omnivore induced a trophic cascade because it fed selectively on the main herbivore rather than plants or algae when both where available (Ho and Pennings 2008; Moksnes et al. 2008). Moreover, both studies also present species cascades involving one major herbivore on one plant or algal species only. In our system, functional complementarity at both the grazer (amphipods and gastropods) and algal (micro-/macroalgae) trophic levels compensated for decreases in the other group. Only when both grazer groups were removed from the system, the total biomass of micro- and macroalgae together increased. Thus, while species cascades may be common in food webs, community level trophic cascades are probably rare in natural communities due to omnivory and within trophic level trait diversity (Polis 1999).

The linking of reduction in top-predators to massive increases of mesopredator populations is common in exploited ecosystems (Eriksson et al. 2009; Ritchie and

Johnson 2009). The impact of mesopredator-release events depends on food web connectivity, where a high number of weak trophic links should decrease the strength of top–down control and reduce the probability of trophic cascades (Dunne et al. 2002; Neutel et al. 2002; Duffy et al. 2007). Our results show that even though omnivores have links to more than one trophic level, the links may be strong and switch in magnitude depending on availability and functional composition of the prey community. For example, Moksnes et al. (2008) suggested that increases in *P. elegans* from large scale decreases in apex predators (*Gadhus morrhua*—cod) have suppressed mesograzer abundances (mainly amphipods) and thereby indirectly contributed to increases in macroalgal production in the coastal zone of the Skagerrak (North Sea). In our study area (the Baltic Sea), substantial mesopredator release events of small-bodied fish have reduced grazing rates, and thereby dramatically increased local biomass production of ephemeral micro- and macroalgae (Eriksson et al. 2009; Sieben et al. 2011). However, the results of the present study suggested that the main impact caused by the presence of *Palaemon* was a decrease in macroalgal diversity, because *Palaemon* was able to include filamentous algae in its diet when palatable grazers decrease. Thus, to predict effects of changing abundances of omnivores, we need to acknowledge that omnivores may have deep vertical effects in food webs by links to several trophic levels. This specifically calls for incorporating properties of the food web, which determine the dynamics between indirect and direct effects of omnivores, such as interactions between the functional diversity on adjacent trophic levels and palatability of prey populations.

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